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Quarantine arthropod invasions in Europe: the role of climate, hosts and propagule pressure

Steven J. Bacon[1,2], Alexandre Aebi[1†], Pierluigi Calanca[1] and Sven Bacher[2*†]

[1]*Agroscope Reckenholz-Tänikon, Research Station ART, 8046 Zürich, Switzerland,* [2]*Ecology & Evolution, University of Fribourg, 1700 Fribourg, Switzerland*

*Correspondence: Sven Bacher, Ecology & Evolution, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland.
E-mail: sven.bacher@unifr.ch

[†]Present address: Laboratoire de Biologie du Sol, Université de Neuchâtel, Neuchâtel 2000, Switzerland

ABSTRACT

Aim To quantify the relative importance of propagule pressure, climate-matching and host availability for the invasion of agricultural pest arthropods in Europe and to forecast newly emerging pest species and European areas with the highest risk of arthropod invasion under current climate and a future climate scenario (A1F1).

Location Europe.

Methods We quantified propagule pressure, climate-matching and host availability by aggregating large global databases for trade, European arthropod interceptions, Koeppen–Geiger world climate classification (including the A1F1 climate change scenario until 2100) and host plant distributions for 118 quarantine arthropod species.

Results As expected, all the three factors, propagule pressure, climate suitability and host availability, significantly explained quarantine arthropod invasions in Europe, but the propagule pressure only had a positive effect on invasion success when considered together with climate suitability and host availability. Climate change according to the A1F1 scenario generally increased the climate suitability of north-eastern European countries and reduced the climate suitability of central European countries for pest arthropod invasions.

Main conclusions To our knowledge, this is the first demonstration that propagule pressure interacts with other factors to drive invasions and is not alone sufficient to explain arthropod establishment patterns. European countries with more suitable climate and large agricultural areas of suitable host plants for pest arthropods should thus be more vigilant about introduction pathways. Moreover, efforts to reduce the propagule pressure, such as preventing pests from entering pathways and strengthening border controls, will become more important in north-eastern Europe in the future as the climate becomes more favourable to arthropod invasions.

Keywords
Biosecurity, climate change, host plant, insects, propagule pressure, quarantine pests.

INTRODUCTION

There is an increasing awareness about the significant threats posed by alien arthropod invasions (Hulme *et al.*, 2009), which are responsible for billions of dollars in economic losses in Europe, negatively affecting a broad spectrum of sectors such as agriculture, forestry and human health (Pimentel *et al.*, 2001; Vilà *et al.*, 2010) as well as threatening biodiversity and ecosystem functions (Kenis *et al.*, 2009). Already over 1000 alien arthropods have established in Europe and are doing so at unprecedented rates (Roques *et al.*, 2010) as globalization continues to remove long-standing abiotic barriers (Levine & D'Antonio, 2002; Pysek *et al.* 2010), and arthropods as a taxonomic group remain understudied in invasion biology (Pyšek *et al.*, 2008). Many factors that influence the likelihood of arthropod invasions have been identified, such as the propagule pressure (Lockwood *et al.*, 2005), climate suitability and host availability (Niemellä

& Matteson, 1996; Leung *et al.*, 2012). However, these factors have mostly been studied in isolation, and knowledge about the relative importance of each of these factors is lacking (Leung *et al.*, 2012). In this study, we address this problem, which could help biosecurity authorities to implement more effective control strategies.

It is generally accepted that the propagule pressure – the number of individuals of an alien species that are introduced to the invaded region is a key determinant of invasion success (Lockwood *et al.*, 2005; Colautti *et al.*, 2006; Wilson *et al.*, 2008). The propagule pressure in alien arthropods is closely linked to international trade (Hulme, 2009; Roques *et al.*, 2010; Bacon *et al.*, 2012), through which arthropods are vectored unintentionally as contaminants and stowaways (Drake *et al.*, 1989; Campbell, 2001; Hulme *et al.*, 2008; Pyšek *et al.*, 2010), making them difficult for management authorities to detect. There are many international agreements aimed at reducing the biosecurity risk of trade, such as the World Trade Organization (WTO) Agreement on the Application of Sanitary and Phytosanitary Measures (SPS), the International Plant Protection Convention (IPPC) of the Food and Agricultural Organization of the United Nations (FAO) and the Convention on Biological Diversity (CBD). Despite these regulations, international transport hubs (Floerl *et al.*, 2009) and the world-wide airline network (Tatem, 2009) play a major role in arthropod dispersal. For example, the western corn rootworm *Diabrotica virgifera* Le Conte (Chrysomelidae; Coleoptera), one of the world's biggest pests of maize, recently invaded Europe around international airports mainly through trade associated with North America (Miller *et al.*, 2005). International trade is important in Europe, as one of the largest importing regions in the world with over half a million flights (FAO 2010; http://www.fao.org) and 500 million tons of maritime cargo (Eurostat 2010; http://epp.eurostat.ec.europa.eu) arriving into Europe from non-European origins annually. Hence, there is a need for a more coordinated defence against invasions in Europe (Hulme *et al.*, 2009).

European countries run a coordinated system of phytosanitary inspection at air and maritime ports of entry. Before exportation, live vegetal goods must comply with international regulations, and a phytosanitary certificate (ISPM 12, 2011) documents the measures undertaken to avoid infestation with quarantine organisms. Upon arrival in Europe, trained inspectors from national plant protection organizations (NPPOs) control the goods. Every positive inspection is recorded in a European database, and the infested goods are destroyed (for a thorough description of the procedure, refer to Bacon *et al.*, 2012).

After the initial introduction, alien arthropod invaders must overcome a continuum of abiotic and biotic challenges to successfully establish in a new region (Blackburn *et al.*, 2011a). Environmental factors in the invaded region such as climate suitability and host availability are also key for successful establishment (Leung *et al.*, 2012).

Alien arthropod invaders are more likely to survive if they are introduced to regions with climatic conditions that are similar to those in their current distribution range (Walther *et al.*, 2009). Temperature is known to be a key limiting factor in their survival, growth and reproduction (Woodward, 1987; Charnov & Gillooly, 2003). Hence, popular climate-matching software based on temperature and precipitation parameters, such as CLIMEX (Version 3, Hearne Scientific Software, Melbourne 2007) and Biomod (Thuiller, 2003), have been used to predict the potential distribution ranges of alien insects based on climatic conditions in their existing and native distribution ranges. For example, CLIMEX models have been used to predict the climatically suitable regions of Europe for many quarantine species listed such as *Anplophora glabripennis* (Macleod *et al.*, 2002) (Cerambycidae; Coleoptera), *Bactrocera dorsalis* Hendel (Stephens *et al.*, 2007), *Ceratitis capitata* Wiedemann (Vera *et al.*, 2002) (Tephritidae, Diptera), *Halyomorpha halys* Stål (Niva & Takeda, 2003) (Pentatomidae; Hemiptera) *Diabrotica virgifera* (Baker *et al.*, 2003), *Leptinotarsa decemlineata* Say (Kocmánková *et al.*, 2011) (Chrysomelidae; Coleoptera) and *Harmonia axyridis* Pallas (Poutsma *et al.*, 2008) (Coccinellidae; Coleoptera).

Host availability is a prerequisite for arthropod survival and reproduction and is thought to be one of the main factors that facilitate invasions of herbivorous arthropods to new environments (Niemellä & Matteson, 1996). It has been hypothesized that invasive species distributions follow their native hosts; for example, the distributions of bark beetles such as *Hylastes ater* Paykull and *Hylurgus ligniperda* Fabricius are closely related to Eurasian and North American coniferous hosts (Brockerhoff *et al.*, 2006).

Despite the propagule pressure, climate suitability and host availability being key determinants of invasion success, however, they have mostly been studied in isolation (Ward & Masters, 2007; Walther *et al.*, 2009; Leung *et al.*, 2012). A better understanding about the relative importance of each of these factors may help predicting invasions with higher accuracy. Such information would be important for European and national biosecurity authorities to implement more effective control strategies. Climate similarity and international trade (measured by air traffic volume) have been analysed in tandem (Tatem & Hay, 2007), but the relative importance of the three factors propagule pressure, climate suitability and host availability in predicting arthropod invasions is lacking.

In this study, for 118 of Europe's quarantine arthropod species in agriculture, we measured for 27 European countries the propagule pressure via agricultural trade, the climate suitability using Koeppen–Geiger climate classifications (including climate change until 2100) and host availability by analysing agricultural host plant distributions. For the 29 most invasive quarantine arthropod species, we tested the relative importance of each of these factors in explaining their European distribution ranges using an information theoretical framework for model selection. Furthermore, we used the results to forecast which arthropod species and which European countries have the highest likelihood of alien arthropod invasions.

We hypothesized that as the propagule pressure, climate suitability and host availability are all known to play a key role in invasion success, then all three factors would be needed to explain quarantine arthropod invasions in Europe. We also expected that under climate change scenarios that predict increases in overall temperatures, Europe in the future would become more climatically suitable for arthropod invasions because a large number of the quarantine arthropod species are of tropical origin (Walther *et al.*, 2009).

METHODS

A full description of methods is given in the online Supporting Information (Data S1).

Propagule Pressure – Trade Volume to be inspected per interception (TVPI)

We quantified the propagule pressure through agricultural trade for 118 quarantine alien arthropod species in 27 European EPPO member states. We used a measure of propagule pressure that we developed and applied in a previous paper (Bacon *et al.*, 2012). In short, agricultural pest arthropods are transported and introduced into new regions mainly via trade of their host plants, that is, crops and crop products. Propagule pressure is related to the volume of plant trade, the probability that arthropods are transported on these plants and the probability that the plant commodities pass border inspections undetected. Trade pathways consist of many components (Hulme, 2009), of which we considered four: country of origin *o*, agricultural commodities being traded *c*, quarantine arthropod species *i* and European destination country *d*, so that each pathway *o-c-i-d* can be uniquely represented. *Trade Volume to be inspected* (TV) to importing European country *d* when importing commodity *c* from origin country *o* was calculated as the value of trade in commodity *c* (in US$), if both arthropod species *i* exist in origin country *o* and commodity *c* is a host. However, only alien arthropods that pass through border controls undetected should be considered for the calculation of propagule pressure. TVPI, the *Trade Volume to be inspected Per arthropod Interception*, is TV divided by the number of border interceptions per *o-c-i-d* pathway and should be interpreted as a measure of the likelihood of quarantine arthropods moving through trade *and* passing through existing border controls – a proxy for the propagule pressure (Bacon *et al.*, 2012).

To calculate TVPI, we obtained trade volumes in US$ in unprocessed agricultural products from the Food and Agriculture Organization (FAO), together with quarantine arthropod distribution and host plant data from the Centre for Agriculture and Biosciences International (CABI) Crop Protection Compendium and the European and Mediterranean Plant Protection Organization (EPPO). We included all European quarantine arthropod interceptions made on agricultural products between 2003 and 2007 (EPPO Reporting Service), which totalled 1168 species-level interceptions (Bacon *et al.*, 2012).

Host availability

We estimated for each quarantine species the area (ha and %) on which agricultural host plants are grown in 27 EPPO reporting European countries (FAOSTAT; averaged between 2003 and 2007). We ignored wild host plants, assuming that the area of wild hosts would be much smaller than that for agricultural hosts.

Climate suitability

We calculated the climate suitability, defined as the match between the physiological tolerance of each quarantine arthropod species and climatic conditions of each European country. To achieve this, we needed to obtain (1) a representation of the climate in each European country, (2) a representation of the climatic requirements of each arthropod species and (3) a method to link country climate to an arthropod climatic profile.

Country climates

We developed a climate-matching approach based on Koeppen–Geiger (KG) climate classifications (Köppen, 1900; Geiger, 1954) updated for the period from 1951 to 2000 (Kottek *et al.*, 2006) (http://koeppen-geiger.vu-wien.ac.at). KG climate classifications have five main vegetation zones (indicated by capital letters), followed by a second letter representing precipitation and a third letter representing temperature (e.g. Cfb represents: warm temperate – fully humid – warm summer, a condition that applies e.g. to most of Great Britain, France, the BeNeLux countries and Germany). From the underlying KG data, we extracted the number of 0.5 degree latitude/longitude grid cells of each climate classification that are contained within each country of the world. These climate classification grid cells were taken as a representation of the climate profile of each country.

Arthropod climatic profiles

We tested two methods for determining arthropod climatic profiles based on their world-wide (non-European) country distribution ranges, for each 118 quarantine arthropod species in agriculture: (1) counting the frequency (number of grid cells) that each KG climate classification occurs across all countries in its distribution range and (2) summing the proportion that each KG climate classification represents in each country, across all countries in its distribution range, that is, weighting the most frequently occurring climates by their relative size within each country. The second method reduces the weight of climate classifications that occur only in few countries that have a wide climatic range (e.g. Russia). The idea behind method (2) is to reduce the weight of climates that occur only in few countries of the arthropod's distribution, because these climates are unlikely to be suitable for the arthropod and to increase weight of climates that are shared by many countries in which the pest species occurs. Both methods determine scores for each KG climate classification per arthropod species, which were then used as weightings.

Linking arthropod climatic profiles to European countries – climate envelopes

After having established which KG climate classifications prevail in each European country and having obtained a climatic profile of each quarantine arthropod species, represented as weightings of KG climate classification using the two methods described above, we calculated a climate suitability for each distinct arthropod–EU country combination based on each of the two methods, using a climatic envelope approach. Step by step, for each arthropod species, this approach involved i) ranking the arthropod's climate classifications by their climatic profile weightings, ii) adding a cumulative sum of these weightings from the highest to the lowest, iii) defining climatic envelope sizes, that is, from a narrow envelope of the top 30% of climates in the cumulative distribution of the climatic profile, to a broad envelope of 90%, in 20% step increments, iv) for each envelope, suitable climates are defined as those KG classifications whose cumulative sum of weightings falls within the defined climatic envelope, that is, in a 90% envelope, the suitable climates are the top-ranked climates whose cumulative sum is < 90%, and lastly, v) for each quarantine arthropod and each climatic envelope size, we calculated the climate suitability as either the absolute number of suitable 0.5 degree latitude/longitude grid cells (or area in ha) or the percentage of suitable grid cells, per European country.

Statistical modelling

We investigated the influence of the explanatory variables: the propagule pressure (TVPI), climate suitability (CS) and host availability (HA) on the distribution of European arthropod species invasions. For statistical modelling, we only considered those 29 quarantine arthropod species (representing 21 families) that have already established populations in at least 2 European EPPO countries (*i.e.* so that they have an existing European range on which to model) and are established in at least 2 non-European countries. We used generalized linear mixed effects models, with TVPI, CS and HA, and all their interactions as fixed effects, and arthropod species as a random effect, to explain arthropod invasions (established or not established, as binomial response) in 27 European countries. We fitted models using the different calculations of the arthropod species climate envelopes: envelope by area (number of grid cells), by percentage of total country area (%) and by proportion weighting of the origin countries, and in each case for envelope size 30%, 50%, 70% and 90%, and finally considering HA by both area (ha) and by percentage of total country area (%), totalling 24 repetitions of model fitting. Models were fitted by the Laplace approximation using the glmer function from the package LME4 (Bates *et al.*, 2012) in R 2.14.1 (R Development Core Team 2012). We estimated parameter values by model selection and averaging (Burnham & Anderson, 2002).

We calculated the *Likelihood of Arthropod Invasion (LAI)* for each distinct arthropod–EU country combination, using each of the parameterized candidate models identified by model selection. The LAIs generated by each candidate model were then weighted according to the probability that each candidate model is the best.

Climate change

The Köppen–Geiger (KG) climate classifications have been further updated to depict climate change projections for each 25-year period between 2000 and 2100 (Rubel & Kottek, 2010), projected using the Intergovernmental Panel on Climate Change (IPCC) A1F1 emissions scenario (fossil fuel intensive) and Tyndall SC 2.03 temperature and precipitation data projections (Mitchell *et al.*, 2004). Data for each of these time periods were applied to our climate suitability calculation method, based on a climate envelope of 90% measured as a percentage of total country area (*i.e.* results Table 1). This analysis was carried out for 44 European countries for which climate data were available, across 118 arthropod species, equalling 5192 distinct arthropod–country combinations of climate suitability comparisons (Table S7). This analysis only considered change in climate suitability and did not include estimates of HA or propagule pressure.

RESULTS

Of all the 156 models fitted, only four had a ΔAICc < 6; all other models had a ΔAICc > 14 and were thus not further considered (Table 1). All four credible models had a 90% climate envelope (i.e. including all KG climate classifications that account for 90% of the counts per country classification of the arthropod species), with climate suitability matched to European countries measured in % of total country area rather than by absolute area in hectares. Furthermore, all credible models included host availability measured in absolute area (ha).

Two of the four credible models were extensions of less complex and better-fitting models (Table 1) and were thus excluded from model averaging (Richards, 2008). The remaining two candidate models both contained the three main effects: the propagule pressure measured by TVPI, climate suitability (CS) and host availability (HA), and the two-way interaction term TVPI:HA. The other two-way interaction terms CS:HA and CS:TVPI were only present in one model each, whilst the 3-way interaction term CS:TVPI:HA was not part of any of the candidate models. Across

Table 1 The 25 best fitting models explaining arthropod invasions in Europe (N = 29 arthropod species), based on the explanatory variables TVPI, climate suitability (CS) and host availability (HA)

			Main Effects			Interactions				
Climate envelope size	Climate suitability units	Host availability units	CS	TVPI	HA	CS TVPI	CS HA	TVPI HA	CS TVPI HA	ΔAICc
90	%	Ha	x	x	x	x		x		0.0
90	%	Ha	x	x	x	x	x	x		−1.9
90	%	Ha	x	x	x		x	x		−2.6
90	%	Ha	x	x	x	x	x	x	x	−3.7
70	Ha	Ha	x	x	x	x		x		−14.0
90	Prop.	Ha	x	x	x	x	x	x	x	−14.4
70	Ha	Ha	x	x	x			x		−14.7
70	Ha	Ha	x	x	x	x	x	x		−15.9
70	Ha	Ha	x	x	x		x	x		−16.1
90	Prop.	Ha	x	x	x	x		x		−16.5
70	Ha	Ha	x	x	x	x	x	x	x	−16.7
90	Ha	Ha	x	x	x			x		−18.3
90	Prop.	Ha	x	x	x	x	x	x		−18.5
50	Ha	Ha	x	x	x		x	x		−18.6
70	Ha	Ha	x		x					−19.3
50	Ha	Ha	x	x	x			x		−19.8
90	Ha	Ha	x	x	x	x		x		−20.1
30	Ha	Ha	x	x	x	x	x	x	x	−20.3
90	Ha	Ha	x	x	x		x	x		−20.3
50	Ha	Ha	x	x	x	x	x	x		−20.6
50	Ha	Ha	x	x	x	x		x		−20.7
90	Ha	Ha	x	x	x	x	x	x		−22.1
50	Ha	Ha	x	x	x	x	x	x	x	−22.3
90	Ha	Ha	x		x					−22.3
90	Ha	Ha	x	x	x	x	x	x	x	−22.4

All models were generalized linear mixed effects models, with binomially distributed response variable. Models are ranked by their ΔAICc value. 'x' denotes whether a variable was included in the model. The two candidate models used for model averaging are highlighted in grey, that is, those whose ΔAICc is less than or equal to 6.0 and whose ΔAICc value is less than the ΔAICc values of all the simpler models within which it is nested.

both candidate models, the host availability had the strongest effect on *likelihood of arthropod invasions (LAI)* in Europe, followed by climate and the three interaction terms (magnitude of coefficients in Table 2). In general, both climate suitability and the availability of hosts had a direct positive effect on the likelihood of arthropod invasions. By contrast, the main effect of propagule pressure (TVPI) was not significantly different from zero. However, propagule pressure did have a positive effect on invasion, but only in highly suitable climates and in conjunction with a large availability of host plants (positive interaction coefficients CS:TVPI and HA: TVPI). A combination of suitable climate and large host availability also disproportionally increased the likelihood of arthropod invasion (interaction CS:HA). Thus, propagule pressure (measured as TVPI) did not increase the likelihood of invasion by itself, but only in combination with other favouring factors.

Using the parameters estimated in model averaging across the 2 candidate models (weighted by their likelihood of

Table 2 Parameter estimates for the two credible models, including mean and 95% confidence intervals for each of the coefficients and model likelihood weightings, for arthropod invasions in Europe

		Confidence interval		Model weights	
	Coefficient	2.50%	97.5%	0.79	0.21
Intercept	−1.622	−2.221	−1.023	x	x
CS (90%)	0.764	0.469	1.059	x	x
TVPI	−0.103	−0.497	0.291	x	x
HA	1.845	1.371	2.320	x	x
CS: TVPI	0.408	0.134	0.682	x	
TVPI: HA	0.612	0.229	0.995	x	x
CS: HA	0.345	0.071	0.620		x

Note that all of the explanatory variables were scaled (subtract mean, divide by standard deviation) so that the coefficients indicate the relative size of their effect on explaining invasions.

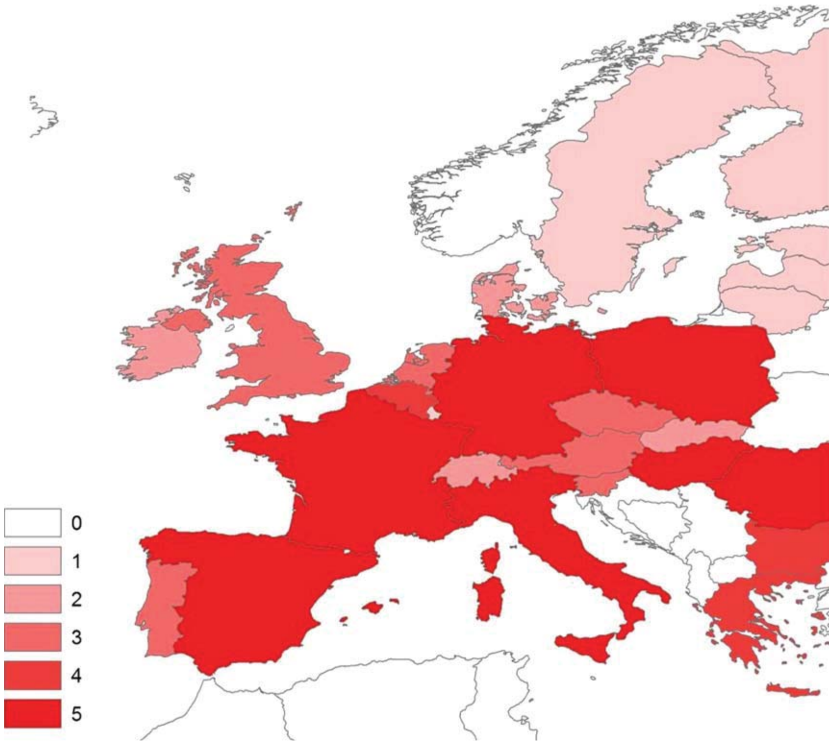

Figure 1 Heat map showing the *Likelihood of Arthropod Invasions* (LAI) in Europe. For each European country, LAI has been aggregated through summation across all 118 quarantine arthropods that have yet to establish in that country. We used a 5-point colour scale; 1 = countries with the lowest 20% of LAI range to 5 = countries with the highest 20% of LAI range (0 = countries not included in the analysis). LAI is calculated as a weighted average of the two candidate models that explain arthropod invasions in Europe.

being the best model, Table 2), we calculated the *likelihood of arthropod invasions* (*LAI*) for each of the 118 quarantine listed arthropod species invading each European EPPO country in Europe, based on actual TVPI, CS and HA, by summing the individual LAI values, for all quarantine species that were not yet established in each country. We found that overall Italy, France, Spain, Hungary and Germany were the most likely countries to be invaded (Fig. 1), and the oriental leafworm moth *Spodoptera litura* Fabricius (Noctuidae: Lepidoptera), the northern corn rootworm *Diabrotica barberi* Smith and Lawrence (Chrysomelidae: Coleoptera), and the sugarbeet wireworm *Pheletes (=Limonius) californicus* (Mannerheim) (Elateridae: Coleoptera) have the highest likelihood to establish in Europe (Table 3).

Overall, climate change is likely to increase the risk of arthropod invasions in Europe. Under the A1F1 emissions scenario, 77% (4021) of the distinct species–country combinations (5192) become more climatically suitable by the period 2076–2100, with a mean climate suitability change of +3.2% ± 0.52% (Table S7). The countries with the greatest increase in climate suitability for quarantine listed arthropod species in agriculture are countries in north-eastern Europe such as Estonia (mean climate suitability change of 49.5% across all 118 arthropod species), Latvia 42.1% and Belarus 33.5%, when comparing KG climate classification from 1951 to 2000 with projected climate classification 2076–2100 (Fig. 2). Over this time period, it is projected that Estonia moves from 27 grid cells in KG climate classification Dfb (polar – fully humid – warm summer) to 22 grid cells Cfb (*warm temperate* – fully humid – warm summer) and 2 grid cells Cfa (*warm temperate* – fully humid – *hot summer*). Likewise, Latvia moves from 34 grid cells Dfb to 24 grid cells Cfb and 12 grid cells Cfa, and Belarus from 112 grid cells Dfb to

Table 3 The *Likelihood of Arthropod Invasions* (LAI) for the top 10 most likely quarantine arthropod invasions in agriculture aggregated across all 27 European countries where the arthropods are not yet present

Rank	Species	LAI	EU Dist.	Country (LAI)	
1	*Spodoptera litura*	19.1	2	Poland	0.94
2	*Diabrotica barberi*	18.3	0	Germany	0.89
3	*Pheletes californicus*	18.0	0	Germany	0.89
4	*Blitopertha orientalis*	16.6	0	Romania	0.91
5	*Myndus crudus*	16.0	0	Italy	0.92
6	*Anthonomus grandis*	15.8	0	Italy	0.91
7	*Spodoptera eridania*	15.7	0	Germany	0.91
8	*Listronotus bonariensis*	14.8	0	France	0.84
9	*Diabrotica speciosa*	14.6	0	Germany	0.91
10	*Epitrix cucumeris*	14.2	1	Poland	0.83

For each arthropod species, the table also shows the current distribution range (measured by the number of European countries the species has currently invaded 'EU Dist.') and the country with the highest LAI.

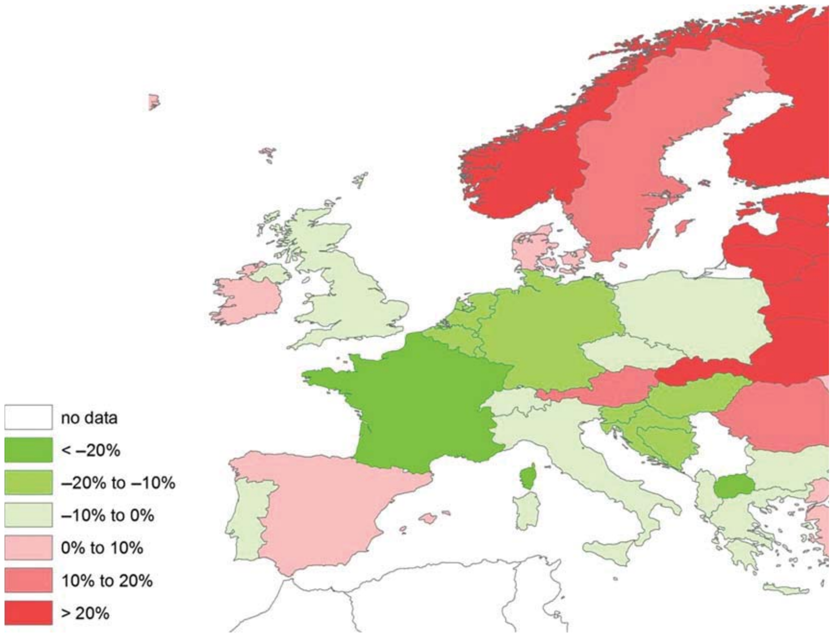

Figure 2 Heat map showing how climate change will impact climate suitability (CS) for arthropod invasions in Europe. For each arthropod–EU country combination, we calculated the absolute difference between current CS and CS in the time period 2075–2100 under the A1F1 emissions scenario. These differences were then averaged over all 118 quarantine arthropod species, to estimate the overall climate change impact to CS per European country. Countries with decreasing CS through climate change are shown in green, and Countries with increasing CS with climate change are shown in red, with a 10% colour step.

3 grid cells Cfb and 109 grid cells Cfa. Hence, moving from polar to warm temperate increases the overall LAI (Table S7).

By contrast, France (mean climate suitability change of −27.5% across all 118 arthropod species), FYRO Macedonia (−21.7%) and Belgium (−19.2%) are projected to decrease the most in suitability for quarantine listed arthropod species in agriculture, that is, France's climate changes from 90% of grid cells in Cfb (warm temperate – fully humid – warm summer) to 53% Csa (warm temperate – *summer dry* – warm summer) and 43% Cfa (warm temperate – fully humid – *hot summer*), reducing LAI (Table S7).

The top three arthropod species to benefit from climate change in Europe are the geranium bronze *Cacyreus marshalli* (Lycaenidae: Lepidoptera; a pest of ornamental *Pelargonium* spp.) (mean climate suitability change of 45.0% across all 44 European countries), the red palm weevil *Rhynchophorus ferrugineus* (Curculionidae: Coleoptera; a pest of palm trees; 28.9%) and the spider mite *Tetranychus evansi* (Tetranychidae: Acari; a polyphagous pest, especially hosts in Solanaceae; 28.9%) (Table S7).

DISCUSSION

Relative importance of propagule pressure, climate suitability and host availability

As expected, the three main effects propagule pressure, climate suitability and host availability were all included in each of the candidate models. However, by far the most important factor in driving arthropod invasions in Europe was the absolute agricultural area of host availability (HA). Hence, countries with larger areas of suitable agricultural host production are more likely to be invaded. This makes biological sense as all arthropods included in this analysis are plant feeders (quarantine in plant protection) and thus dependent on the presence of their food plants. Note that HA measured as a percentage of total country area was not included in any of the candidate models, indicating that the absolute area of hosts is a better predictor of invasions. Some of the quarantine arthropods are known to feed also on non-agricultural plants, and wild hosts may therefore increase the availability of hosts. Because information on the distribution of wild hosts was missing, only planted crops were used to evaluate the availability of hosts. However, we do not expect that wild hosts would substantially change our findings, because they are usually far less abundant than agricultural plants. True host shifts, that is, an arthropod species feeding on a plant outside its known host range, are very rare and unpredictable and therefore should not affect our conclusions.

Climate-matching at the European scale played a major role in explaining arthropod invasions, as expected (Woodward, 1987; Charnov & Gillooly, 2003), despite agricultural practices such as the use of glasshouses and irrigation techniques, dramatically altering the prevailing climatic conditions. Climate was the second most important factor in our analysis as a main effect and also interacted significantly with the propagule pressure and HA. In general, broad climate envelopes which included a wide range of climate classifications better explained invasions, that is, narrow envelopes excluded much of Europe as climatically unsuitable. Hence, using a broad 90% envelope and count data for arthropod profiles created enough data variation to explain arthropod invasions.

Surprisingly, the propagule pressure measured by TVPI had a positive effect in invasion success only in interactions with HA and CS. In fact, the two-way interaction with host availability is the third most influential factor in the model. These interactions demonstrate that propagule pressure becomes increasingly important the better the climate matches the arthropod's requirements and the larger the food source. Of course, invasion success depends on whether an arthropod is able to survive in the invaded region, and propagule pressure is only the first step. In general, the positive two-way interactions between TVPI, host availability and climate-matching mean that the overall effect on the likelihood of invasion is greater than the sum of the main effects would predict. Thus, studying each factor in isolation will give a misleading picture about its importance (Walther *et al.*, 2009); a combination of factors interacts in driving the invasion process. To our knowledge, this is the first demonstration that propagule pressure interacts with other factors to drive invasions and is not alone sufficient to explain arthropod establishment patterns. These findings might help in solving the current debate about the importance of propagule pressure in establishment success (e.g. Blackburn *et al.*, 2011b; Moulton *et al.*, 2012).

We found that, in general, climate suitability (CS) in Europe will increase overall, especially in north-eastern Europe, based on the A1F1 climate change scenario, which will increase LAI. This was expected as a large number of the quarantine arthropod species in plant protection are of tropical origin and would be more suited to rising European temperatures. However, climate change influences biological invasions in numerous ways (Dukes & Mooney, 1999; Walther *et al.*, 2009). For example, in addition to removing physiological constraints, climate change can affect insect dispersal – by altering insect flight patterns (Battisti *et al.*, 2006), phenology (Harrington *et al.*, 2007) and atmospheric circulation patterns which affect long-range dispersal of some insects (Greenslade *et al.*, 1999), and arthropod establishment – by altering the dynamics of community structure and ecosystem functioning (Walther *et al.*, 2002; Parmesan, 2006). Furthermore, climate change will also indirectly impact HA and the propagule pressure, by changing agricultural production and trade patterns in Europe. Therefore, climate change will have a greater and wider impact than increasing overall CS in Europe.

Implications for biosecurity

Importantly from a biosecurity perspective, some of the key factors for invasion such as HA and the propagule pressure can be modified and adapted. Some examples of methods to reduce HA, other than lowering absolute production levels, could be to create buffer zones between agricultural production areas and transport hubs (*i.e.* invasion hotspots; Floerl *et al.*, 2009) or arthropod migration routes, that is, maintaining host-free areas around airports and alongside major transport pathways to lower the establishment risk of the most feared invasive arthropods. Note that this also includes managing the availability of wild hosts that have not been considered in this study because data are not available. Other measures including integrated pest management and biotechnological advances could also be applied to reduce HA, that is, the EU recommends regular crop rotation as key element of IPM against the establishment and further spread of the western corn rootworm *Diabrotica virgifera* (Chrysomelidae; Coleoptera) in Europe (European Commission, 2006).

Although biosecurity authorities cannot affect the overall prevailing climatic conditions, they can monitor artificially heated agricultural areas such as glasshouses, which can dramatically increase CS, for new upcoming pests. For example, many quarantine arthropod pests that cannot yet establish in the field in Europe have successfully invaded glasshouses, such as the notorious western flower thrips *Frankliniella occidentalis* Pergande (Thripidae: Thysanoptera) (Roques *et al.*, 2010). Over the longer term, because climate change will increase the CS, a global effort to reduce the impact of climate change will likely benefit Europe from an invasion biology perspective (Walther *et al.*, 2009).

Our results suggest that reducing the propagule pressure combined with HA and CS would have an even greater effect on LAI because of their significant interactions. Therefore, efforts to reduce the propagule pressure, such as strengthening border controls and reducing the contamination risks of international trade (Bacon *et al.*, 2012), are important now and even more so in the future as Europe becomes more climatically favourable for arthropod invasions.

Our findings can directly be implemented in pest risk assessments (PRAs) and thus also have some important implications for policy. Legislation regarding quarantine arthropod species lists is currently set at the European level; however, with LAI varying between arthropod-EU country combinations, quarantine species lists and point of entry controls could be more efficient if they were country-specific according to LAI. Our results enable national plant protection organizations (NPPOs) to tailor quarantine species lists and inspection strategies specific for their countries risks. Countries in north-eastern Europe should also be aware that climate change will increase their LAI, and hence, the role of border controls will become more important to them. By contrast, central European countries might experience less pressure from quarantine species due to decreased climatic suitability (less precipitation). Furthermore, the LAI of final destination of shipments should be considered during phytosanitary inspections because of Europe's 'first point of entry' approach to inspection and the free flow of intra-European trade. This would require more broadly accessible and detailed invasion data and specific training for inspectors.

We quantified for the first time the risks of establishment of quarantine arthropod species in Europe due to propagule pressure, HA and CS. Our results can be directly used by decision makers at the European level to develop guidelines for border inspections that go beyond simple lists of quarantine species. Such guidelines should be based on current and future underlying risks of different pathways. It is also advisable to implement a system of quality control of inspections, for example, by also reporting negative inspections (Bacon *et al.*, 2012). It is important that Europe makes a more united approach to tackling invasions (Hulme *et al.*, 2009), with an understanding of the specific risks to each member state.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Host availability for the Tobacco Whitefly *Bemisia tabaci* in Europe.

Table S1 TV, TVPI and interception data for 118 arthropods in Europe.

Table S2 Climatic profiles for the Tobacco Whitefly *Bemisia tabaci*.

Table S3 Climate suitability for the Tobacco Whitefly *Bemisia tabaci*.

Table S4 Change in climate suitability for *Bemisia tabaci* under climate change.

Table S5 Data used for model fitting.

Table S6 Models explaining arthropod invasions in Europe.

Table S7 Climate suitability for all species-country combinations for each 25 year time period between 1975 and 2100.

Data S1. Full description of Materials and Methods.

This paper is part of the PhD thesis of SJB. All authors are interested in biosafety research, in particular of alien insects, their consequences for society, and methods to detect and prevent invasions. (http://www.unifr.ch/biol/ecology/bacher, http://alexaebi.wordpress.com).

Author contributions: A.A, S.B and S.J.B conceived the study; S.J.B. compiled the data, designed and conducted the analysis. S.B. performed the statistical analysis, and P.C. helped to design the climate analysis. The manuscript was written by S.J.B., with guidance from A.A. and S.B.